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ABNORMALITIES IN THE CESTODE MONIEZIA EXPANSA. III.

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In Parts I. and II. of this paper (Child, '00) the various abnormalities occurring in *Moniezia expansa* were described, in Part I. those consisting of imperfect and partial proglottids and in Part II. the spiral abnormalities. It now remains to determine the manner in which these various abnormalities arise, and to discuss the significance of the facts observed.

As is clear from preceding descriptions, there is not the slightest evidence that any of the form-variations of the proglottids appear after development of the proglottid is begun. The degree of differentiation of all parts of an abnormal proglottid is the same, and corresponds to its position in the chain. All the various kinds of form-variations occur in the youngest distinct proglottids. These facts lead to the conclusion that the variations in form appear at the time when the proglottid is formed; that imperfect and partial proglottids and spiral series take their origin in that part of the body in which the causes that lead to the formation of proglottids are at work. That is to say, variations in form are the result of variations in the original formative processes, not the result of modification in the form of structures already established.

Since this is the case, the process of formation of the normal proglottid may be expected to throw some light upon the factors concerned in the formation of abnormalities. The first part of this paper is devoted to a description of the normal method of proglottid-formation.

The figures are all semi-diagrammatic, but in the figures of sections the nuclei of the parenchyma were drawn in with the

camera, and thus correspond as nearly as possible in number and position with those in the actual sections. The subcuticular layer, however, is represented schematically by stippling.

1. Structure of the Neck-Region and Formation of Proglottids.

Behind the scolex there is a region some five to eight millimeters in length, commonly known as the neck, in which no division into proglottids is visible externally.

A few words regarding the structure of the body in this region will render the following description somewhat clearer.

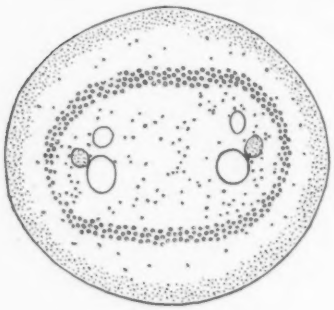


Fig. 42.

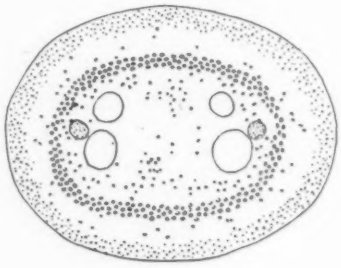


Fig. 43.

Figs. 42 and 43 are transverse sections through the region between the scolex and the point where distinct proglottids appear. Fig. 42 is taken from a section near the scolex, Fig. 43 from one further back. The lines 42 and 43 in Fig. 46 (p. 98) indicate respectively the approximate levels of the two sections. The proglottids are just becoming visible externally at the posterior end of Fig. 46.

The outer cuticular membrane is indicated by the line bounding the figures. Beneath this is a cellular layer, the subcuticular layer, with rather closely packed nuclei, indicated schematically in the figures by the stippled region beneath the cuticle. At this stage of development the nuclei appear to lie in more than one row. Beneath this cellular layer is found the parenchyma. The portion of the parenchyma external to the longitudinal muscles I have, for convenience, designated as the peripheral parenchyma

(Rindenschicht of various authors). This contains a few widely scattered nuclei. The most conspicuous muscle-layer at this stage is the well-developed longitudinal muscle-layer indicated in the figures. Other muscles are not shown. Within the muscle-layer the central region of the proglottid is occupied by parenchyma. This portion of the parenchyma surrounded by the longitudinal muscle layer may be called the central parenchyma (Mittelschicht). In it lie the large ventral and the smaller dorsal nephridial canals and the lateral nerve cords.

In the central parenchyma the nuclei are more abundant than

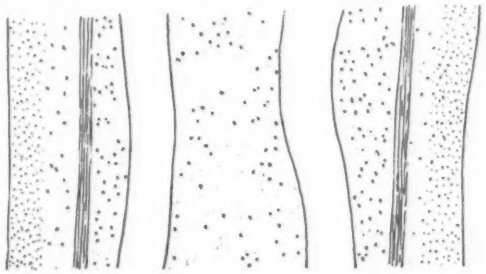


FIG. 44.

in the peripheral layer, and, as the figures show, they are rather more numerous in the outer parts of the parenchyma, especially between the nephridial canals and the muscle-layer.

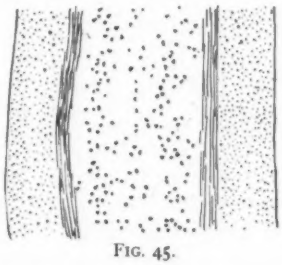


FIG. 45.

The two longitudinal sections, Figs. 44 and 45, show the same structures. Fig. 44 is drawn from a frontal section about half way between the scolex and the first distinct proglottids in the plane of the line 44, Fig. 53 (p. 103). Here the nuclei of the

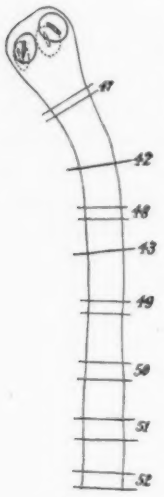


FIG. 46.

central parenchyma are seen to be more abundant at the two sides between the nephridial canals and the muscles. In Fig. 45, which is taken from a sagittal section in the median line (see line 45, Fig. 53, p. 103), the nuclei of this region are seen to be most abundant near the outer boundary of the central parenchyma.

The earliest stages of the growth of the body occur in the neck-region and the proglottids appear at the posterior end of the neck.

Consideration of the method of proglottid-formation requires, therefore a study of the neck-region, and to this the following paragraphs are devoted.

The series, Figs. 47–52, show parts of the neck and the region just posterior to it, viewed as transparent objects. The region of the neck represented by each figure is indicated approximately in Fig. 46 by the numbered areas enclosed by parallel lines, the number in each case corresponding to the number of the figure. All six figures were drawn from a single preparation, a whole mount of scolex and neck-region, which was fixed in the extended condition while slightly flattened between two slides. The longitudinal muscle-layer is indicated by parallel broken lines, and the nephridial canals are drawn in. Nuclei and their general distribution are represented by the stippling.

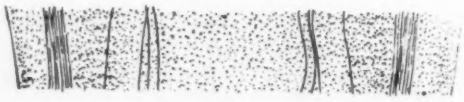


FIG. 47.

In Fig. 47, which shows the region at the posterior end of the scolex itself, the nuclei in the region between the nephridial canals and the longitudinal muscles, where they are most abundant, show faint indications of an arrangement in parallel bands, groups, or zones extending transversely. The groups of the two sides of the body appear to be entirely separate from each other,

the inner end of each band or zone lying in the region of the nephridial tubes. The groups or aggregations of nuclei are so indefinite that it is difficult to count them or to determine whether they correspond on the two sides of the body. The nuclei of the region between the nephridial tubes show no definite grouping.

FIG. 48.

Fig. 48, taken further posteriorly (see Fig. 46), shows a similar arrangement of the nuclei within the longitudinal muscle layer.

This peculiar arrangement of nuclei in this region varies somewhat as regards distinctness in different specimens. It can always be made out in preparations which are well extended longitudinally, but in contracted specimens the nuclei are so massed together that it often disappears. The examination of a large number of specimens has, however, satisfied me that it is a normal characteristic of this region.

Fig. 49 is taken from a point near the posterior end of the neck region (see Fig. 46) and shows bands of nuclei extending across the central parenchyma, the first distinct evidences of pro-

FIG. 49.

glottid-formation. The arrangement of the nuclei in these bands is probably due not so much to migration of the nuclei as to more rapid multiplication of certain of them, thus forming aggregations. It may be, however, that migration does occur to some extent. From this point on, these parallel bands of nuclei become more and more distinct and it is clearly evident that they represent the proglottids.

In Fig. 50 an arrangement of nuclei into transverse bands extending across the central parenchyma is still more distinct and

the bands are broader than in Fig. 49. As yet, however, there is no trace of the inter-proglottidal furrows upon the margins or surfaces of the body, and indeed the grouping of the nuclei does not extend into the peripheral parenchyma at all.

FIG. 50.

Fig. 51 shows a still later stage in the process of proglottid-formation. The bands of nuclei are still broader and more distinctly marked in the middle region of the body, though the nuclei are still more abundant in the lateral regions of the central parenchyma. It is evident that the number of nuclei is increasing. One marked advance in the development is noticeable here, viz., the arrangement of the nuclei in the peripheral parenchyma in groups corresponding to those formed within the longitudinal muscles. It is evident that this grouping is gradually extending toward the surface of the body, though it has not yet reached it.

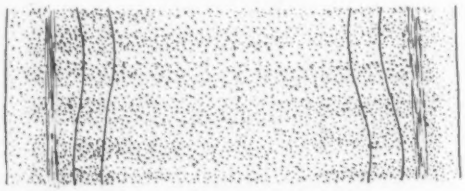


FIG. 51.

In other words, there are in this region of the neck localized regions of growth, or regions in which the nuclei multiply more rapidly than in the intervening, regions and now these areas of more rapid growth are gradually extending toward the surface of the body. All of the figures being drawn to the same scale, it is evident that the growth in width of the body has begun.

In Fig. 52 the proglottids are well defined and their boundaries are indicated upon the surface by shallow furrows. The body is

increasing in width and each proglottid is growing longer as well. Even at this stage the nuclei are seen to be more abundant in the region of the nephridial canals.

The Figs. 49–52 render it sufficiently evident, I think, that each proglottid is simply an area of relatively rapid growth in the parenchyma. The growth first becomes evident in the lateral regions of the central parenchyma, *i. e.*, between the nephridial canals and the longitudinal muscles, where, as was noted above, the nuclei are most abundant. It gradually extends from each side across the middle region of the body, thus forming a zone, which at first includes only the central parenchyma, but gradually extends to the peripheral parenchyma. At last the growth be-

FIG. 52.

comes evident upon the surface, the regions in which it occurs becoming convex as might be expected. At this stage then each proglottid represents a transverse slice of the body which is increasing in size more rapidly than the intervening regions, which therefore become marked as furrows. The furrows are not to be regarded as constrictions, but simply as marking the areas where growth in the transverse direction is least rapid.

The important points in the process are as follows: Each proglottid arises as two distinct aggregations of nuclei, one on either side of the body, which later extend toward the median line and become continuous, and still later extend to the surface or at least to the outer layer of the body.

In Figs. 47 and 48, as noted above, there are traces of a transverse arrangement of the nuclei in the lateral regions of the central parenchyma into bands or groups. The question at once arises as to whether these groups represent the earliest stages of the proglottids, or whether they are connected with some de-

tail of the structure of the neck-region. The evidence on this point is gathered and discussed in the following paragraphs, in which the structure of the neck-region and the early proglottid is examined in detail.

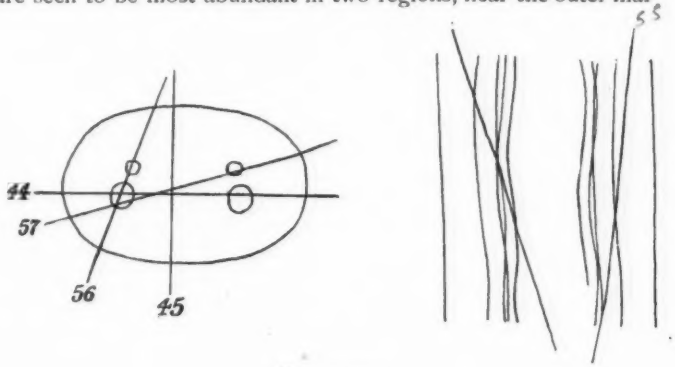
Attention may once more be called to the fact that in the figures of sections the individual nuclei, except those of the subcuticular layer, were drawn in with the camera, so that the arrangement of the nuclei seen in the figures corresponds as closely as possible to their arrangement in the actual section. As the nuclei are distinct and not very numerous, the figures are probably free from serious inaccuracies in this respect.

First of all in this connection, the two transverse sections, Figs. 42 and 43 (p. 96), require renewed consideration. These sections lie in the plane of the aggregation of nuclei and consequently do not show them. Incidentally it may be mentioned, however, that in following through a series of transverse sections from the neck-region, the nuclei between the nephridial canals and the longitudinal muscles are more abundant in some sections than in others and that a certain, not very marked periodical recurrence of the two conditions can be made out. The point of immediate interest shown in Figs. 42 and 43 is the greater abundance of nuclei in the lateral regions of the central parenchyma. In both figures the regions contain numerous nuclei distributed with more or less uniformity, while the region between the two pairs of nephridial canals, though showing some more or less distinct aggregations, contains in general fewer nuclei. This point confirms the evidence afforded by the study of whole mounts, viz., that the nuclei appear to be more abundant in the lateral regions of the central parenchyma than elsewhere when viewed from either surface. Of course in whole mounts the distribution of nuclei in the central parenchyma is more or less marked by the subcuticular peripheral nuclei.

Longitudinal sections are necessary to show the groups of nuclei. The frontal section, Fig. 44 (p. 97), is taken from near the anterior end of the neck. It passes through the ventral nephridial canals. The plane of the section is indicated by the line 44 in Fig. 53. The nuclei of the central parenchyma are seen to be much more abundant lateral to the nephridial canals

than between them. Moreover, an indistinct arrangement in groups of the nuclei of these lateral regions of the central parenchyma does appear, especially on the left side. The groups of nuclei are so illy defined in the preparations in toto, where the whole dorso-ventral thickness of the central parenchyma is seen, that it can scarcely be expected that a section only a few micra (7) in thickness, and thus containing only a small part of the total number of nuclei in a given group, should show the arrangement any more clearly. The nuclei of the peripheral parenchyma are very few in number and scattered, showing no indication of any arrangement in groups corresponding to those of the central parenchyma.

In Fig. 45, a sagittal section near the median plane, the nuclei are seen to be most abundant in two regions, near the outer mar-



FIGS. 53–54.

gins of the central parenchyma, appearing in the section as two longitudinal bands of nuclei, which are in reality sections of two layers of nuclei, a dorsal and a ventral layer. These layers were indicated indistinctly in the transverse sections shown in Figs. 42 and 43. The tendency to aggregation of the nuclei into groups which is present in the lateral regions of the central parenchyma is not visible here, or at least not sufficiently distinct to appear in the section. As regards this point the section confirms the observations on the whole mounts. The region from which this section was taken corresponds approximately to the region from which Fig. 48 was drawn, being probably a little posterior to it.

In Fig. 48 the groups of nuclei, though visible laterally, do not extend to the median plane. It should be noted that the parenchyma-nuclei are more abundant in Fig. 45 than in Fig. 44, thus indicating that multiplication of the nuclei is occurring even in the neck-region anterior to the point where the proglottids be-

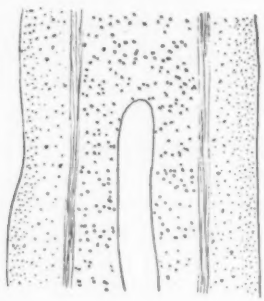


FIG. 55.

come distinct, for Fig. 45 is taken some distance posterior to Fig. 44.

Fig. 55 is drawn from a nearly sagittal section near the posterior end of the neck region. Its plane is indicated by the line

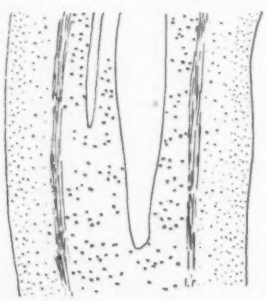


FIG. 56.

55 in Fig. 54. The ventral nephridial canal lies partly in the plane of the section. Here again an aggregation of the nuclei into groups is visible, especially in the lower portion of the figure.

Fig. 56 represents another oblique section which cuts both

nephridial canals. It is taken from about the same region of the neck as Fig. 55, but from another individual. The plane of this figure is represented approximately by the line 56 in Fig. 53. In this figure the grouping of the nuclei is more distinct than in the other longitudinal sections.

These figures represent sections of approximately the same region as is shown in Fig. 49, *i. e.*, a region in which the proglottids first become recognizable. The groups of nuclei represent, therefore, the early stages of what we know to be proglottids, and yet the chief differences between these figures and Fig. 44 consist in the larger number of nuclei and a greater degree of distinctness in the groups of the former figure.

At this point the relation of the lateral groups or zones of nuclei in the anterior neck region to the proglottids requires consideration.

As is evident from the facts stated above, the distinct proglottid extending across the body and marked by a convex contour of the surface appears first at a considerable distance behind the scolex. All through the neck region, however, occur the indistinct groups of nuclei in the lateral regions of the central parenchyma, and, when the proglottids form, their earliest stages appear to arise from the groups.

If these groups represent the earliest stages of proglottid-formation, then the proglottid must be laid down just behind the scolex and pass backward through the neck-region in consequence of the formation of new proglottids in front of it, until finally its development reaches a stage where it becomes visible externally. If the groups of nuclei anterior to the regions where proglottids first become recognizable as bands of nuclei extending over the nephridial canals toward the median plane, do not correspond to proglottids, they must be due to some other features in the structure of the neck. In this case, the neck constitutes an unsegmented region, which gradually becomes marked off into proglottids.

The facts favor the second view. In the first place, the groups of nuclei are just as distinct immediately behind the scolex as they are further back (*cf.* Figs. 47 and 48), *i. e.*, no development occurs in them except perhaps a slight increase in the number of

nuclei until the region is reached where the proglottids become distinguishable. And secondly, I have found similar groups of nuclei in the neck-region of other cestodes, but in a number of cases they did not correspond to proglottids, but a number of them, four or five or perhaps more, were included within a single proglottid when it formed, and a still higher number were found in older proglottids. The examination of *Moniezia expansa* alone might lead to the acceptance of the first of the two alternatives stated above, for when the proglottids do appear they are aggregations of nuclei in the lateral regions of the central parenchyma, of about the same size as the other groups. This comparison with other forms shows that the indistinct grouping of nuclei throughout the neck region has nothing to do with the formation of proglottids. The existence of the groups is probably due to the more or less regular repetition of the dorso-ventral muscles, which are most abundant in the lateral regions of the central parenchyma, and perhaps also in part to the arrangement of the circular muscles. Between the muscles the nuclei of the undifferentiated parenchyma are aggregated into groups. Such an arrangement seems to be visible in some sections, but in others does not appear distinctly.

I have considered this point rather fully because in *Moniezia* the resemblance of the nuclear groups to the early stages of the proglottids is very close.

Returning to the consideration of the forming proglottid, we find that after it becomes visible as a zone of nuclei extending across the central parenchyma, a continuous increase in size in all directions occurs. Some of the features connected with this process of growth require attention here.

In the early stages of the proglottid, before the furrows have become visible on the surface of the body, the parenchyma-nuclei are multiplying very rapidly. Fig. 51 shows the general appearance at this stage, and Fig. 57 is a section of the same stage in the plane of the line 57 in Fig. 53. Here the nuclei of the peripheral parenchyma are just beginning to appear in groups, corresponding in position to the lateral regions of the proglottids in the central parenchyma. Although in whole mounts the boundaries of the proglottids are well marked, sections

show them less clearly. It is interesting to note that the grouping of the nuclei in the peripheral parenchyma appears first in the lateral regions as represented in Fig. 57. Sagittal sections of this stage near the median plane show no grouping of the peripheral nuclei there, although in the central parenchyma the boundaries of the proglottids are quite distinct. Here again the earliest

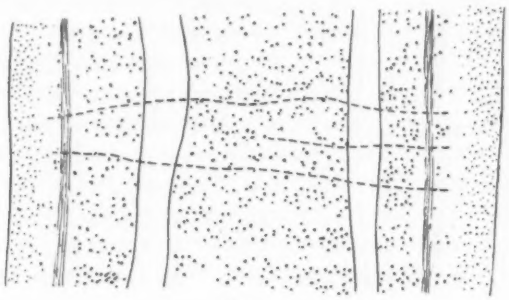


FIG. 57.

stages of development appear near the main nerve-cords and extend gradually to the other parts.

A little later the boundaries of the proglottids become visible on the surface (Fig. 52), and sections at this stage show still further increase in the number of nuclei, especially in the central parenchyma. Fig. 58 represents a sagittal section near the median line. The furrows are beginning to appear on dorsal and ventral surfaces. The outlines of the proglottids are distinct within the central parenchyma and the transverse nephridial canals have appeared. The scarcity of nuclei in the peripheral parenchyma is noticeable, but the few present are more or less distinctly grouped.

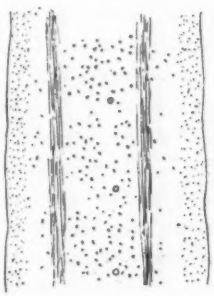


FIG. 58.

A somewhat later stage is represented in the frontal section, Fig. 59. Here the subcuticular cells, which are represented schematically by the dotted region at the margin, have become indistinctly grouped, the spaces between the groups corresponding to the inter-proglottidal furrows. The

peripheral parenchyma-nuclei, though few, are grouped in the proglottids.

Now the proglottid is completely established as a localized region of growth. Later changes which occur lead to some alteration in the shape and proportions of various parts and to the differentiation of various organs within the proglottid.

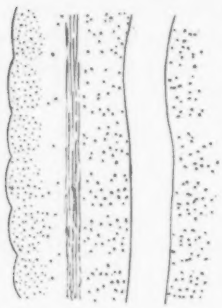


FIG. 59.

In some Cestodes, including *Moniezia*, the longitudinal nerve-cords are connected by a series of transverse proglottidal commissures and other proglottidal nerves are also present. The development of this proglottidal nervous system has been investigated but little, although it is certainly a field of considerable interest. The time at which the nerves appear, their relation to the formation of other parts of the proglottid and themanner of their differentiation are all difficult but important problems.

Tower ('00) has described and figured the origin of the transverse commissures in the neck-region of *Moniezia* (Fig. 1, Taf. 21). Mr. Tower has had the kindness to inform me personally that the folds along the margins of the neck in this figure are not intended to represent the outlines of proglottids but are merely the folds resulting from contraction. He finds that the transverse commissures begin to appear before the proglottids are distinct, but he has not been able to discover any great degree of regularity in the order of their appearance. The first traces of these commissures appear almost immediately behind the scolex, but their formation is not completed until the stage where the proglottids begin to be visible. It is possible, as Tower himself admits, that further study might show a much greater regularity in the development of these commissures.

The point in Tower's figure where the first traces of the commissures appear is certainly far anterior to the region in which the proglottids become distinct, *i. e.*, the commissures are apparently the first of all the proglottidal structures to appear.

The study of the neck-region of *Moniezia* brings to light a

number of facts which possibly indicate a close relation between the appearance and early development of the proglottids and the nervous system. The figures of whole mounts (Figs. 47–52) and of transverse and longitudinal sections through the neck region (Figs. 42, 43, 45) show that the earliest aggregations of the parenchyma-nuclei occur in the region in which the lateral longitudinal nerve-cords lie, and that growth of the proglottids follows the lines which the transverse dorsal and ventral commissures must take as they develop.

In the transverse section, Fig. 43, the nuclei of the central parenchyma are mostly situated in an indistinct ring around the outer margin of the central parenchyma. In Fig. 42, from a more anterior region, this arrangement is less clearly marked. In the longitudinal sagittal section near the median plane (Fig. 45), which is taken from a region posterior to Fig. 43, the same arrangement, or more rapid multiplication of the nuclei is evident in the outer region of the central parenchyma, *i. e.*, in the region which the dorsal and ventral portions of the nervous system occupy.

In general it is evident then that the multiplication of the parenchyma-nuclei occurs most rapidly in regions of the body about the nervous system.

Too little is known regarding the arrangement and development of the proglottidal commissures and nerves in other Cestodes to enable us to determine whether the proglottidal system appears before the proglottids become distinct.

A number of authors have described the nervous system of the proglottids of various cestodes, but little attention seems to have been paid to the region of formation. It seems extremely probable, moreover, that our knowledge of the proglottidal system is incomplete as regards most cestodes. The difficulty of distinguishing with certainty the nervous tissue, not the lack of interest in the subject, is responsible for this condition. Branches arising from the longitudinal nerves have often been mentioned and among the later writers upon the subject a number (Koehler, '94; Scheibel, '95; Lühe, '96; Cohn, '98), have discovered in various forms more or less complex systems of commissures between the longitudinal nerves, sometimes forming a highly developed net-

work. So far as I am aware, the only account of the development of this system is the one given by Tower ('00).

Lühe ('96) and Cohn ('98) have stated that in *Ligula*, where the reproductive organs are repeated but the body shows no segmentation, and in *Schistocephalus*, a segmented form, systems of ring-like and radiating transverse commissures connect the numerous longitudinal nerves. The two sets of commissures always occur together, but are said not to be segmentally arranged. Nothing is known, however, of the development of these commissures, and indeed it is not even certain that other nerves do not exist.

Mr. Tower has very kindly informed me that in abnormal proglottids of *Moniezia* the nervous system was not normally arranged. Unfortunately his notes, drawings, and preparations were destroyed by fire.

It appears then from the little we know of the nervous system of cestodes, and its development in the proglottids, that the system of commissures makes its appearance very early in the history of the proglottid. Tower's account of the nervous system in the neck-region of *Moniezia* renders it very probable that the proglottidal commissures constitute the earliest visible indications of proglottid-formation. As noted above, the nuclei of the central parenchyma in the neck are more abundant in the region of the lateral nerve-cords and in a dorsal and ventral layer which corresponds closely in position to the region occupied by the dorsal and ventral parts of the nervous system. Each proglottid begins to form in two separate parts, one in the region of each lateral nerve-cord; these two parts extend toward the center and unite, *i. e.*, they follow in general the same course of development as do the dorsal and ventral transverse commissures (Tower '00, Fig. 1, Taf. 21). A little later the process of proglottid-formation extends to the peripheral parenchyma; the small nerves extending toward the surface of the body appear, according to Tower, somewhat later than the commissures. Still later in the history of the proglottid the genital organs appear. Tower found certain nerves which he designates as genital nerves, and states that these appear later than the other portions of the nervous system. All of these facts certainly indicate a close connection between the development of the nervous system and that of the proglottid.

It would be premature to attempt with the few facts available to reach a final conclusion with respect to the relations of the two processes. There are three possibilities to be considered: the localization of growth and the formation of proglottids may be the result of the appearance of the transverse nerves and commissures and other parts of the proglottidal system; the development of the nervous system may be the result of the appearance of proglottids; or lastly, both may be effects of a common cause. Which of these three possible views is correct, it is impossible at present to decide. If the first of the three be accepted and it be admitted that some stimulus from the parts of the nervous system as they develop leads to the formation of a proglottid, an explanation is afforded of the first appearance of the proglottid as two groups of nuclei on opposite sides of the body, of the position of these groups, of the direction of their growth and of the order of development of the various parts of the proglottid. It would be out of place here to discuss the influence of the nervous system on growth, differentiation, and regeneration in general, but that such an influence has been found to exist in many cases cannot be denied.

If we accept either of the other two possibilities, no explanation of the observed method of proglottid-formation can be given at present.

The development of the nervous system and the process of proglottid-formation in different cestodes certainly offers a most interesting field for research.

2. The Growth of the Proglottids.

The further history of the proglottid concerns its growth in size, various alterations in shape and the development of the genital organs. It is beyond the scope of this account to enter into

Figs. 60.

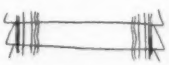


Fig. 61.

the details of the formation of the genital organs, but some features of the growth require consideration.

Figs. 60–63 are outline drawings of the form of the proglottid

at various stages of its history. Fig. 63 shows one half of the proglottid. The longitudinal muscles and the nephridial canals are indicated. Examination of this series will show clearly that

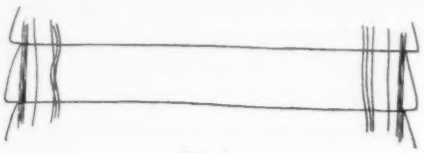


FIG. 62.

almost the whole increase in the width of the proglottid is due to the growth of the central parenchyma, the peripheral parenchyma forming little more than the posterior extensions at the margins.

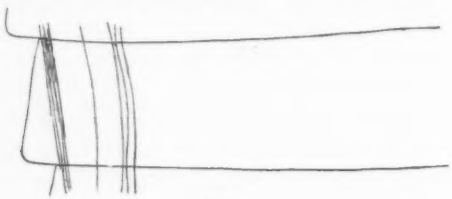


FIG. 63.

In the growth in thickness of the body, *i. e.*, in the dorso-ventral direction, the central parenchyma is not so markedly predominant. The three regions seen in a sagittal section preserve

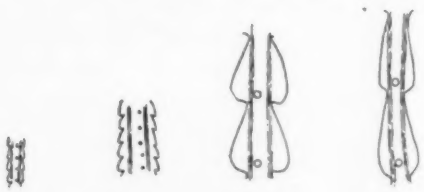


FIG. 64. FIG. 65. FIG. 66. FIG. 67.

much the same proportions during the growth of the proglottids (Figs. 64–70). In this series Figs. 66 and 67 show respectively the contracted and extended conditions in proglottids of the same age. Figs. 68 and 69 show similar conditions in a later stage. Fig. 70 is from a nearly "ripe" proglottid. In this series it is seen that the peripheral parenchyma has undergone about the

same amount of growth here as at the lateral margins, while the central parenchyma shows very little relative increase in thickness.

In general, the central parenchyma grows chiefly in the lateral and longitudinal directions, the actual increase in thickness being much less than the increase in other dimensions and relatively very slight. The growth of the peripheral parenchyma increases

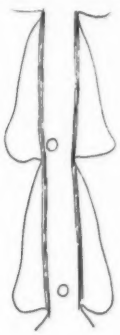


FIG. 68.

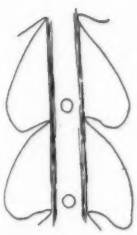


FIG. 69.

FIG. 70.

in amount from the anterior to the posterior end of each proglottid, but is similar about the whole circumference of the body. The first traces of the posterior extensions of the proglottids are seen in Fig. 71, a sagittal section of an early stage. Nearly all the nuclei of the peripheral parenchyma are grouped near the posterior boundary of each proglottid, indicating that growth is more rapid there than elsewhere, and the outlines of the proglottids are no longer regularly rounded, as in Fig. 59 for instance, but show distinctly localized growth in the posterior region.

The above observations upon the origin and growth of the proglottid may be summed up as follows: The whole neck is a region of growth; in the anterior part of the neck the growth is general but posteriorly it gradually becomes localized and thus gives rise to the proglottids. Each proglottid arises as two distinct aggregations of nuclei in the central parenchyma near the lateral nerve-cord. Gradually the intervening portions of the central parenchyma come to show a similar arrangement and a zone of localized growth is formed. This growth next extends

to the peripheral parenchyma and finally becomes visible on the surface in the rounded contour of the proglottid and the furrows marking it off from others. Later growth, while including all parts of the proglottid, is greatest in amount in the central parenchyma. The relative increase in length and width of the

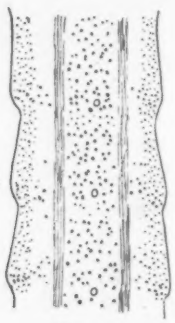


FIG. 71.

proglottid is considerably greater than its increase in thickness. The folds forming the posterior borders of the proglottids are formed by the localized growth of the peripheral parenchyma, and since growth begins here considerably later than in the central parenchyma, these folds are comparatively late in making their appearance.

(*To be continued.*)

SOUTHEASTERN UNITED STATES AS A CENTER OF GEOGRAPHICAL DISTRIBUTION OF FLORA AND FAUNA.

CHAS. C. ADAMS.

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INTRODUCTION.

From a faunal standpoint, southeastern United States, exclusive of Florida, is very remarkable. The fauna is not only very rich in individuals and species, but also in endemic forms. Some of these are indigenous, while others are evidently fragments of an ancient and formerly widespread fauna. Another fact which increases our interest is the general relationship of this fauna to that of the Northeastern United States, both biologically and geographically, since there can be but little doubt that this area, together with the boreal region, contains the most important centers of distribution for Eastern United States since the Glacial Period. Some of these characteristics are likely to escape notice unless we consider the fauna in its entirety, and not as restricted by geographical limits.

Many of the characteristics of this fauna have long been recognized. It has been well established that the temperate fauna and flora of Northern United States were driven *south* before the ice of the Glacial Period, and that with the retreat of the ice to the

north, a northward migration of life took place. I have hoped that the Postglacial centers of dispersal could be more definitely located than simply in the South, and I have found from a study of geographical relationship of the fauna and flora that one important center has been in *Southeastern* United States, with Chattanooga as the approximate center.

Geographical Affinities of the Temperate Fauna and Flora of Eastern United States.

Several years ago my attention was first attracted toward the Southeast in attempting to get some idea as to the probable geographic origin of our Illinois reptilian and amphibian fauna. I was then led to conclude that this fauna was primarily of *southeastern origin.* At the same time I learned that the flora of the upper Mississippi valley came from the Southeast. MacMillan ('92, p. 653) said of the Minnesota valley, with respect to its higher seed plants: "While continentally central, it is by no means botanically central, but is peculiarly an Atlantic coast and southern region." With regard to the species he says (ibid., p. 717): "As a whole the metaspermatic flora of the Minnesota valley presents itself as distinctly eastern and southern by species as before by genera."[1] Dr. Bessey ('92 and '00) has shown that the trees and shrubs of Nebraska came from the Southeast. He says: "A close study of the foregoing facts as to the distribution of our woody plants shows that nearly all have probably migrated to the plains from the east. . . . Nearly all our trees have come up the Missouri bottoms and spread from the southeastern corner of the state west and northwest." The trees of Kansas clearly show the same origin, as is easily seen by comparing Mason's ('92) list of Kansas trees with the one given by Dr. Bessey.

Cope ('96, p. 895) has pointed out the Eastern origin, or center of distribution, of our fish, amphibian, and turtle fauna. Upon closer analysis this fauna will undoubtedly indicate a *southeastern origin.* I have not been able to learn that students of birds and mammals have especially noticed that Southeastern

[1] By reference to a good contour map of the Mississippi valley, it will be easy to see the highway by which this flora reached this region from the Southeast.

United States is a center of dispersal, yet one can hardly doubt that such will prove to be the case, upon investigation. The annual paths of bird migrations favor this idea. One more illustration will be taken from the fauna. Mr. Bryant Walker's ('98, p. 10) study of the Unionid fauna of Michigan clearly shows that this fauna is almost entirely of Mississippi River origin, and the Mississippi River Unionid fauna is well known to be of *southeastern origin*. But it is not necessary to multiply instances, because the same law holds for the bulk of our fauna and flora and will be recognized by one familiar with any fairly large group of animals. The affinities of both fauna and flora thus point to, and converge toward the Southeast. About the only marked *exceptions* to the rule are the distinctly *northern* or *boreal* groups.

Such illustrations as the foregoing are significant and sufficient to show that to the Southeast is a region deserving of special attention from a faunal standpoint. Because it is believed that here is the natural starting point for an attempt to untangle many faunal and floral problems, evidence has been collected which seems to throw light upon some of its peculiarities.

Richness, or Abundance and Diversity of Life.

As an illustration of the abundance of life, I will consider the flora, which shows a luxuriant development. Sargent ('84, p. 4) says: "Upon the slopes of the southern Allegheny Mountains, and in the valley of the lower Red River, regions of copious rainfall and rich soil, the deciduous forest of the continent attains unsurpassed variety and richness."

The richness of the fauna is shown by both the abundance and size of the individuals. Binney ('85, p. 34) has called attention to this in the case of the land shells of the "Cumberland Subregion" of the southern Appalachians. He says: "If to the 39 species catalogued above as peculiar to this subregion, are added the 69 which inhabit it as a portion of the interior region, it is seen that in the Cumberland subregion we find the largest number of species of any portion of North America. The subregion is equally prolific in individuals, and the individuals are highly developed."

The fresh water molluscan fauna is even richer than the land

shell fauna. Mr. Charles T. Simpson, of the U. S. National Museum, has told me that within 200 or 300 miles of Chattanooga there are more valid species of Unionidæ than in all the rest of the world. As to the Pleuroceridæ, about 300 or 400 species are found in this same area. These and the Viviparidæ here reach their largest size. Here also is the maximum differentiation of the crayfish. The states of Georgia, Alabama and Tennessee, have, according to Faxon ('85, p. 179), the richest crayfish fauna—36 species.

The vertebrate fauna is also very rich. Jordan ('96, p. 114) says of the fish fauna: "These conditions [favorable for fish] are all well realized in the Washita River of Arkansas, in the various tributaries of the Tennessee, Cumberland, and Ohio, and in these streams, among the American streams, the greatest number of species have been recorded."

Endemism and Relicts in the Fauna.

There is still another line of evidence which indicates that this region is not only a recent center of dispersal, but in addition, an area of preservation of ancient types. While it is in this region that the indigenous fauna of Eastern United States reaches its greatest development, it is not these forms primarily to which I wish to call attention now, but to the *relicts* or fragments of a still more ancient fauna. For convenience these will be discussed in two groups:

1. *Relicts having Asiatic Affinities.*—Years ago Asa Gray ('78), and Hooker ('79), and more recently Sargent ('94), have discussed the close relationship existing between many plants found in Eastern America and others found in Japan or Eastern Asia. This discontinuous distribution of many of these forms indicates that they are fragments of an ancient flora. Hooker says: "This generic identity, however, gives but a faint idea of the close relationship between East American and East Asiatic, especially of the Japanese floras, for there is further specific identity in about 230 cases, and very close representation in upwards of 350; and what is most curious is that there are not a few very singular genera of which only two species are known, one from east Asia, the other in east America." The tulip tree (*Liriodendron*), bald

cypress (*Taxodium*), sweet gum (*Liquidambar*), and tupelo or sour gum (*Nyssa*) are interesting examples of genera limited to Eastern Asia and Eastern North America.

But little attention has been given to the Asiatic relationship of the fauna of Eastern United States. No case has come to my notice of a mammal or bird which is limited to *southeastern* United States and shows close East Asiatic affinities. The rodent genus *Zapus* is solely American excepting a single species in Western China (Miller, '00, p. 112). The isolated East Asiatic relative (*Sialia cœlicolor* Hods.) of our common blue bird (*Sialia sialis* L.) is interesting in this connection (Seebohm, '81, p. 328). But our alligator has a near relative in China. The salamander fauna (Gadow, '01, p. 95) of Eastern North America is the richest in the world. *Triton*, as in the case of the dragon-fly *Boyeria*, mentioned below, occurs in Eastern United States, Europe and Eastern Asia. The genus *Amblystoma* is abundant in Eastern North America and has only a single species in Eastern Asia. But the most interesting case among the salamanders is that of the hellbender (*Cryptobranchus allegheniensis*) whose only near relative is the giant salamandar (*C. japonicus*) of Japan, which attains a length of over five feet. Among fish, Cope ('75, p. 64) gives three genera, the spoon-bill (*Polyodon*), the carpsucker (*Carpiodes*) and a catfish (*Ameiurus*), each represented in China with one species; and Jordan ('96, p. 100) gives the shovel-nosed sturgeon (*Scaphirhynchus*) with relatives in Central Asia.

Among crustacea, the occurrence of *Limulus* upon the Atlantic coast with relatives in Asiatic waters and the freshwater *Peneus* in Eastern United States and also at the foot of the Himalayas (Semper, '81, p. 437), are to the point. Huxley, in his "Crayfish" (p. 334), has pointed out a similar relation among crayfish. Faxon ('85, p. 176) says, concerning this relationship: "The Cambari of Eastern United States are mostly related, not to the crayfishes on the other side of the Rocky Mountains, nor to those on the opposite shore of the Atlantic, but to those of the remotest district, Eastern Asia."

Among insects we have some interesting relicts. For example, we have a dragon-fly (*Hagenius brevistylus*) with its nearest

relative in Japan, and also *Boyeria*, with three species, one species each in Japan, United States and Europe. Our luna moth (*Tropæa luna*) has a close relative in China (*selene* Leach). The Bryozoan genus *Pectinatella*, although mainly of Northern distribution in the United States, has two species, one in Eastern United States, and the other (*P. gelatinosa*) in Japan.

This oriental relationship has been clearly pointed out with regard to some of our Unionidæ by Simpson ('96, p. 330). He says: "The Naiad fauna of this region [Oriental] is magnificent and diversified, and almost rivals that of the Mississippi Valley in vigor, size, solidity and variety of forms. Both Dr. C. A. White and von Ihering believe that the Unios and Anodontas of this area are closely related to those of the central part of North America. Not only does there seem to be a general relationship among a large number of the Naiads of this province with those of the Mississippi basin, but several oriental groups are apparently so close to those of our own region that it is well-nigh impossible to separate them. Thus, the Asiatic Anodontas, typified by *A. woodiana* Lea if found in the United States, would be placed by most students with *A. plana;* the Chinese Unios of the group of *U. housei* Lea, and *myersianus* Lea, are evidently quite near the *Alatus* assemblage; *Unio superbus* Lea, is very much like our *U. capax* Green, and a number of the tuberculate forms of China could almost be placed in the American groups of *U. lachrymosus* and *U. pustulosus*." As has been said before, it is well known that the Unionidæ fauna of the Mississippi River system has been derived from that of Southeastern United States. It is important to notice that the East Asiatic affinities are so distinctly marked in the case of the *fresh water fauna*.

The same explanation which Asa Gray gave for the flora, doubtless holds for the fauna. In Preglacial times the flora had an extensive boreal distribution, as shown by Greenland fossils; and with the advance of the ice, life was driven South in both hemispheres, and has been preserved in both, in favorable localities. An analogous case in the other hemisphere is the preservation of certain mammals in Africa and in the Oriental region (Osborn, '00, p. 57) and Unionidæ (Simpson, '96, p. 340).

Relicts not Showing Asiatic Affinities.

Among animals, there are not only members of this fauna showing close Asiatic affinities, but there are other relicts which do not show such a relationship. Jordan ('88, p. 168) has given a number of genera of lowland fish which he considers archaic forms, or members of an ancient fauna. The mud minnow (*Umbra*), the pirate perch (*Aphredoderus*), the pygmy sunfishes (*Elassoma*), and the blind fishes (Amblyopsidæ), are examples of such forms. Among butterflies *Libythea* is of this type also, and *Tachopteryx* among dragon-flies, and doubtless many other insects are.

Two Centers of Dispersal in Southern United States.

That the South was a retreat for life during the Ice Age is too well known to be discussed here. On account of the great amount of endemism and relicts in the Southeast it seems fair to conclude that quite an abundant and diversified fauna and flora lived there during the Ice Age, although the contrary opinion is often expressed. In south temperate North America there seem to be two very distinct and powerful centers of dispersal, or centers of "adaptive radiation," as Osborn ('00, p. 49) might call them. One, to which we have been calling attention, is in the Southeast, and the other in the Southwest on the arid plateau of Mexico and Southwestern United States. This latter area, or distinct center of dispersal, has a very large number of indigenous forms, as is shown by Merriam's system of zoögeographical areas ('93, p. 401). This is undoubtedly the area where the characteristic arid fauna (and flora)[1] of North America has originated or has had its center of dispersal. The great amount of endemism in this area has suggested that this may have retained much of its present arid condition for a considerable period of time, possibly preceding and during the Ice Age; and one condition of its present richness may be due to its greater distance from the ice-sheet which destroyed many forms in Southeastern United States. The heavy rainfall and forests of Southeastern United States should be contrasted with the arid plains and deserts of the Southwest and the corresponding difference in the types of animals originating in these two regions, noted.

[1] Gray, '81, p. 62, and Bray, '00, p. 713.

Northeastern United States during the Ice Age evidently could have had only a boreal fauna and flora. The present distribution of the boreal fauna and flora is along the northern border of the United States and the higher parts of the Appalachian Mountains. But it is not this element with which we are primarily concerned, because we have seen that the biogeographical affinities of the forms which at present dominate in the Northern United States east of the Great Plains do not point to a boreal origin, nor to the arid region of the plains, nor to the Southwest, but to the *Southeast.*

The criteria, which have been used to determine this center of dispersal will next be considered.

Criteria for the Determination of Centers of Dispersal.

In attempting to determine centers of dispersal of animals, I have found it necessary to keep clearly in mind the tests which are legitimate for such determinations. In a very large number of cases we do not have paleontological evidence in sufficient abundance to materially aid us. For this reason I have thought it desirable to state the criteria used.

1. Location of greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms (Allen).
4. Location of maximum size of individuals (Ridgway-Allen).
5. Location of greatest productiveness and its relative stability, in crops (Hyde).
6. Continuity and convergence of lines of dispersal.
7. Location of least dependence upon a restricted habitat.
8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.
9. Direction indicated by biogeographical affinities.
10. Direction indicated by the annual migration routes, in birds (Palmén).

Some of these tests have long been utilized, but, so far as I have been able to learn, all have not been definitely used for this particular purpose. The fifth (productiveness) is very closely related to the second (dominance). It is very well known that

often plants and animals taken from their indigenous country to a new one, require a very favorable habitat in order to live. Hollick ('93, p. 196) and Cowles ('01, p. 105) have called attention to certain plants of more general distribution in the South, which in the North occur only under very favorable or restricted conditions. This change of habit and habitat with divergence from the center of dispersal is a subject worthy of special attention. If Osborn's law of adaptive radiation is of general application, we should expect just such a change in habitat as has been noticed to accompany the divergence from the original home.

The eighth deserves some special attention on account of the present active interest taken in the study of individual variation, to which reference will be made later. The direction of biogeographical affinities and convergence of lines of dispersal, as has been shown, first called my attention to the Southeast.

Outlets or Highways of Dispersal from the Southeast.

Next in importance to the centers of origin themselves are the highways from and to these regions. From the Southeast we have several very well-marked outlets, as follows:

1. The Mississippi Valley, and valleys of tributary streams: the leading outlet.

2. The Coastal plain, leading along the Atlantic seaboard northward, and along the gulf coast to Florida, and the Southwest.

3. The southern Appalachians and adjacent plateaus, forming an outlet to the North.

These are the principal paths of dispersal; two are lowland, one is upland. The lowland highways have functioned not only for the Southeast, but also for the fauna of tropical origin, as Webster ('98, p. 72) has shown to be the case for the chinch-bug, which has pushed into the United States via Florida and the West Indies and also from Mexico. Of course, these outlets may serve also as inlets from other regions.

Aquatic life has been greatly favored by the Mississippi River system. From the Southeast, the Tennessee River has undoubtedly been the leading outlet; and next, perhaps, the Cumberland River. Formerly the ancient Appalachian River (*i. e.*, the Tennessee above Chattanooga plus the Coosa-Alabama River)

in the Appalachian Valley, was an important highway for aquatic life, and the valley remains to the present time a highway for land forms.

Desirability of Studying the Variations or Modifications in Animals and Plants as They Diverge From Their Center of Origin Along Their Lines of Dispersal.

With the increased interest which is now being shown in the study of individual variations of plants and animals, it is of value to see the relation which such studies have to the highways of dispersal, and vice versa. The real importance of this relation does not seem to be fully realized. This fact is apparent when the geographical variations are largely expressed in terms of the cardinal points, instead of in their relation or deviation from the center of dispersal or changed environment. On account of the topographical relations and past climatic changes of our country, most of the migrations have been deflected more or less to the North or South, and thus such expressions apply in general.

A few points will be mentioned to which special attention is directed:

1. Variation in size, its diminution from the central area. Allen ('76, p. 310) has shown that in North America birds and mammals of austral origin tend to increase in size to the South, while those of boreal origin tend to decrease in size. How general the application of this law is among other animals, has yet to be determined, nor is it known how much the paths of dispersal may influence this. This seems to show concentric divergence from the center of origin. Allen ('71, p. 92) has also called attention to important variations in the size of "peripheral organs" in birds, such as the tail, beak and claws. Weed ('92 and '93) has published two interesting papers on the geographical variations of the harvest-spiders, which show that they increase in size of body and length of legs to the South.

Jordan ('93, p. 23), in speaking of the increase in the number of vertebræ in fish toward the North, says: "In most cases, as the number of vertebræ increases, the body becomes proportionally elongate. As a result of this, the fishes of the Arctic waters are, for the most part, long and slender, and not a few of

them approach the form of eels. In the tropics, however, while elongate fishes are common enough, most of them (always excepting the eels) have the normal number of vertebræ, the greater length being due to the elongation of their individual vertebræ, and not to their increase in number." The relation of these changes to paths of dispersal appears to be close, in some cases at least, as Jordan ('01, p. 566) emphasizes that there is a North and South trend of the lines of distribution of shore fishes.

2. Very closely related to the above law of size and that of dominance of a type in its native home is another formulated by Hyde ('96, p. 575) of the U. S. Department of Agriculture, concerning the productiveness of crops. He says: "Entirely independently of whether the average yield per acre be high or low, the nearer the approach to the region to which a product is indigenous, the more uniform will be the rate of production from year to year; and the farther the departure from such region the greater the liability to fluctuation. This law clearly indicates the greater stability in the indigenous area, and increased variability, with departure from that center. The close relation of the law of size and Hyde's law of productiveness indicates a general tendency which is surely of considerable economic as well as scientific importance, especially with regard to the introduction and acclimatization of foreign plants and animals.

3. The continuity and directness of the individual variations along diverging lines of dispersal is of considerable importance. This fact was impressed upon me by the study of a very extensive collection of gasteropod shells from many localities in the Tennessee River system.[1] There are two very distinct types of shells, which intergrade more or less, in a progressive way, as one passes down stream from the head-waters; one extreme type being in the head-waters and the other farther down stream. It is the degree of continuity or progressiveness in the deviation of the characters which clearly points in definite directions, and emphasizes the necessity of a study of series taken along the lines of dispersal.

In the case of the land fauna the situation is much more complex, yet if highways of dispersal are considered analogous to

[1] Proc. A. A. A. S., 1900.

streams, we are furnished with a good working hypothesis, since the convergence of these lines points to a center of dispersal.

4. The study of variation is essentially a study in biological dynamics, because the lack of stability is the very characteristic considered. The close relation between centers of origin and highways of dispersal emphasizes the desirability of considering faunal and floral areas from the same dynamic standpoint. By this method we can understand the relationships and form of these areas much better. Such areas are *dynamic centers* from which tension lines and zones radiate; and the genetic relationships of these areas can only be determined by a study of the present and past dynamic relations. An important step was made in this direction when Gray and Merriam (Merriam, '90, p. 24) recognized that our North American flora and fauna are composed of *two elements*, boreal and austral, each tending to move from its center of origin.

From a dynamic and genetic standpoint, the limits and significance of life areas take on a new meaning and importance when, as it were, we stand at the center or focus of dispersal, and look outward. From this point of view we look upon the life of a region as constantly diverging or radiating from its original home and the parental stock, encountering new conditions of environment and becoming modified in both habits and structure. The continuity in variations, which is one of the most marked characteristics in the geographical variations, can be safely determined only by the study of the form along its highways. The paths of dispersal are the lines along which we may expect the hereditary factors to show their influence most distinctly. Again, these paths bear the same relation to each other as the branches of a phylogenetic tree, and may therefore be compared with such branches. In phylogenetic studies the most fruitful results do not come from a comparison of the tips of the different branches but from a study and comparison of forms along the same branch and therefore of common descent.

We may with advantage carry this comparison still further, and consider the genetic relationships which faunal areas bear to each other. The lines of kinship are shown primarily along the lines of dispersal. Here, as before, it is not to the relationships which

exist between the terminal branches on which we are to focus our attention, but to those affinities which exist along the highways toward the center of origin. The double origin of the North American fauna and flora will illustrate the present standpoint. The lines of dispersal may be represented by two trees, one with its roots in the North, and the other with its roots in the South, and whose branches intermingle. From these two centers, life has radiated in all possible directions, but on account of the North and South trend of the topography the lines of dispersal have, in the main, been North and South. For this reason the general lines of kinship are likely to be most strongly expressed in these same directions.

It is a very fundamental law that most forms of life are confined to restricted areas and only a small number have extensive distribution. Thus, from the centers of origin there is a constant decrease, or *attenuation* in the number of forms which have been able to depart far from the original home. From this standpoint, therefore, the question arises as to what criteria are to be used in the determination of life areas. Should more stress be laid upon the concentric relations, or degree of attenuation, from the center of dispersal, or, on the other hand, upon the genetic affinities, such as exist along the lines of dispersal? Are the natural affinities better expressed zonally or dendritically? In one case the tree is horizontally truncated and in the other the branches are torn apart.

Surely the genetic and dynamic standpoint, which attempts to explain the life of an area in terms of its origin, favors, as a working hypothesis, a trial of the dendritic method. The method of work here suggested will put faunal studies upon a *distinctly genetic basis.*

From the relationship which exists along the lines of dispersal, we draw an important practical conclusion. In collecting a series of animals for the study of variation, one of the first things to be done is to determine its means and highways of dispersal and then secure material from along these lines. This will greatly simplify the study of land forms, because in this manner we have a clue to determine which localities are likely to be the most important, and upon these we may concentrate our attention.

5. The geographical distribution of color variations is a subject which it is very desirable to study from the standpoint of geographic origin as well as from that of climatic influences. Allen ('71, '72, '74, '77 and '92), especially, has given much attention to the formulation of the laws of geographic color variation among North American birds and mammals, and correlates some of these variations with that of moisture. Ridgway ('72) has also an important paper on color variations in birds. Keeler ('93) and Hasbrouk ('93) are referred to for further information on color variations. These papers give numerous cases showing that species of wide distribution change in color in different localities. These papers cannot be discussed here, but deserve to be much better known.

Summary.

First. In general the fauna and flora of Northern United States East of the Great Plains are geographically related to those of the Southeast and this geographical relationship points to an origin in the direction of the Southeast except in the case of the distinctly boreal forms.

Second. The abundance and diversity of life in the Southeast indicates that it has been, and now is, a center of dispersal.

Third. The relicts indicate that the Southeast has been a center of preservation of ancient types, and the endemism shows that it has been a center of origin of types.

Fourth. There are two distinct Southern centers of dispersal in temperate United States; one in the moist Southeast, and the other in the arid Southwest.

Fifth. Ten criteria, aside from fossil evidence, are recognized for determining the center of origin or the locality of dispersal:

1. Location of the greatest differentiation of a type.
2. Location of dominance or great abundance of individuals.
3. Location of synthetic or closely related forms. (Allen.)
4. Location of maximum size of individuals. (Ridgway, Allen.)
5. Location of greatest productiveness and its stability, in crops. (Hyde.)
6. Continuity and convergence of lines of dispersal.

7. Location of least dependence upon a restricted habitat.

8. Continuity and directness of individual variations or modifications radiating from the center of origin along the highways of dispersal.

9. Direction indicated by biogeographical affinities.

10. Direction indicated by annual migration in birds. (Palmén.)

Sixth. There are three primary outlets of dispersal from the Southeast:

1. The Mississippi Valley and its tributaries.

2. The Coastal Plain.

3. The Appalachian Mountains and adjacent plateaus.

The first two have also functioned for tropical types, and the third for boreal forms. Dispersal is both forward and backward along these highways.

Seventh. The individual variations of animals and plants, such as size, productiveness, continuity of variation, color variation, and change of habit and habitats, should be studied along their lines of dispersal and divergence from their center of origin. Life areas should be studied as centers of dispersal and origin, and hence *dynamically* and *genetically*.

HULL ZOÖLOGICAL LABORATORY,
UNIVERSITY OF CHICAGO, December, 1901.

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THE INTERNAL INFLUENCES THAT DETERMINE THE RELATIVE SIZE OF DOUBLE STRUCTURES IN PLANARIA LUGUBRIS.

T. H. MORGAN.

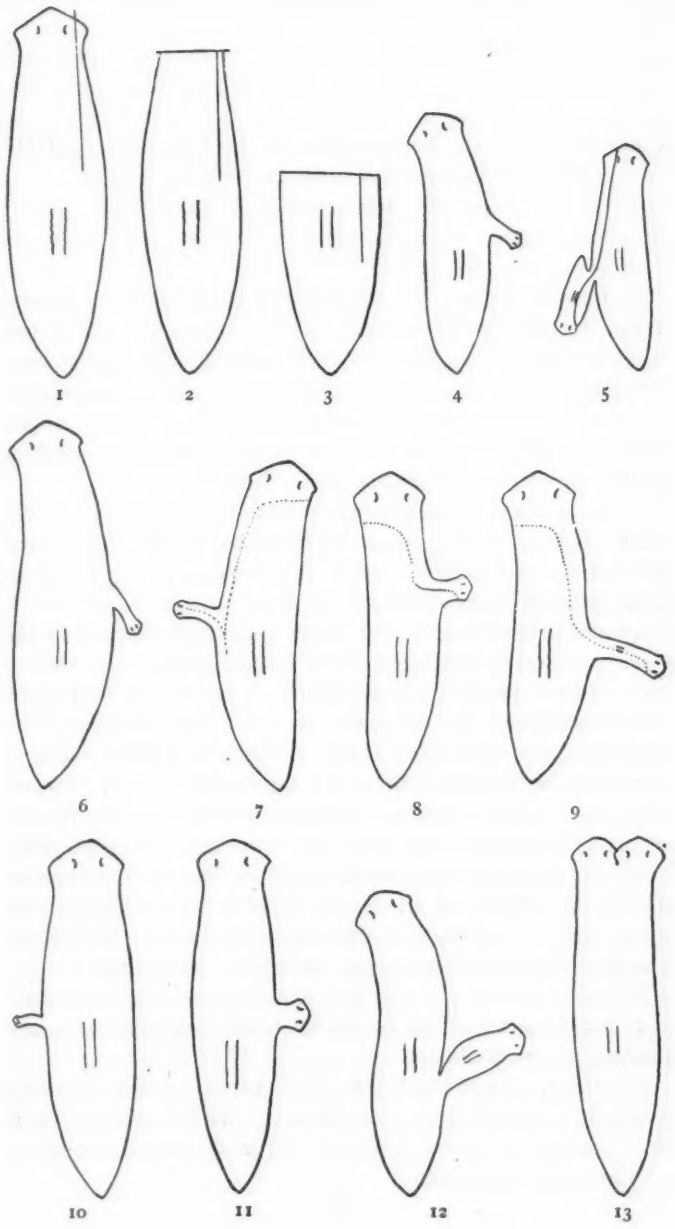
In a previous paper[1] I attempted to determine what internal factors regulate in planarians the limit of size of each of two heads when such are present. Two conditions appeared to have an influence on the result: (1) The width of the region connecting the part to the rest of the organism, (2) the length of the new part. By the following experiments I have attempted to gain the further insight into the conditions:

In one series the planarians were split lengthwise into unequal parts, as shown in Fig. 1; or else the head was first cut off, and then the posterior piece was split lengthwise, as shown in Fig. 2. Under both of these conditions the head on the smaller piece is much smaller than that on the larger part. The purpose of the experiment was to see if by abundant feeding the size of the smaller head could be brought up to that of the larger; or whether its size is determined by the width of the region connecting the small head with the larger piece. If the longitudinal cut does not extend as far posteriorly as the old pharynx, a new pharynx does not, as a rule, come into the smaller part. If, however, the cut is extended posteriorly as far as, or beyond, the old pharynx, a new one may come into the small part. The same end can be reached by cutting off the worm in front of the pharynx as shown in Fig. 3, and then splitting the posterior piece lengthwise. The side piece will be, of course, shorter in the last case.

The results show that the size that the new smaller head attains is determined largely by the presence or absence of a new pharynx in the small part.

The following cases will serve to illustrate some of the ways in which the regeneration takes place. A narrow piece was split off in one case as shown in Fig. 1. A small head developed at

[1] *Roux's Archiv*, XIII., 1901.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its anterior end, but there was no pharynx present. The small piece was attached to the main body at the side and just in front of the anterior end of the pharynx, Fig. 4. Five months later it had not grown any larger (although the worm was kept well fed), but, in fact, appeared to be smaller than at first, Fig. 6. In two other cases the split had extended so far back that a pharynx developed in the small piece, Fig. 5. A tail also grew out at the new side behind the new pharynx. Subsequently the two pieces pulled apart. In another series the old head was cut off by a cross-cut, and then a split made down one side, right or left, Fig. 2. The condition of the two heads a month and a half later is shown in Figs. 7, 8, 9. In the first and second cases a pharynx is absent, but in the third a pharynx has developed in the middle of the smaller worm. The latter condition of these three worms, five months after the operation, is shown in Figs. 10, 11, 12. In the first the head at the side is smaller than it was before ; in the second it has remained about the same size ; while in the third, which contains a pharynx in the smaller piece, the head and the piece as a whole have increased in size.

In another series the heads were split exactly in the middle line. In some of these the split was made only in the anterior end—the cut not extending posteriorly to the pharynx—in others the cut extended into the pharynx region. In other cases the head was first cut off and then the worm split in the middle line. When the head was split for only a short distance, each half completed itself—if the parts were kept from reuniting—as shown in Fig. 13. The head remained smaller in size than the normal head, and even after seven months had not increased any further in size. The inner sides of the heads were a little smaller in size than the other. If the split extends further posteriorly[1] the new heads become larger than in the last case, but still not full size, Fig. 14.

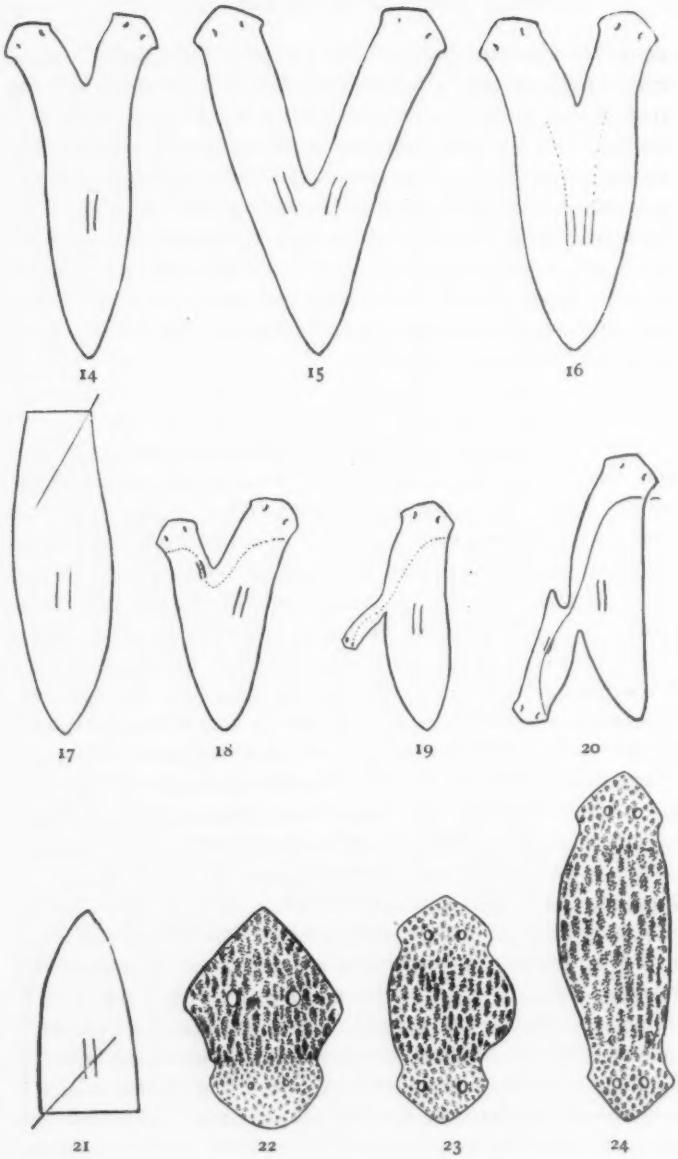
If the cut extends into the region of the pharynx so that two proboscides are formed, one in each half, Fig. 15, the two new heads appear to become larger than in the preceding case, but still do not attain full size. Each appears to be proportionate in size to the part of the body on which it is found, and its size is

[1] The old head had been first cut off.

determined by that of the rest of the part. If the latter should grow to the normal full size the heads would, no doubt, also become full size. Since the parts would become full size if they were separated from each other the explanation of their failure to enlarge beyond a certain size is unquestionably connected with the fact of their union with each other. Very often the pieces partially reunite after the operation, and two proboscides are formed as shown in Fig. 16. In such cases the body at, and beyond, the region of the proboscis is broader than normal, and in consequence the heads at the anterior ends may be larger than when only a single proboscis is present, as in Fig. 14.

In order to see how important a factor the extent of the surface regenerating a head is, as compared with the size of the area of union of the parts, the following experiment was made. The old head was first cut off, and then by an oblique cut, as shown in Fig. 17, a triangular piece was partially cut off. Pieces of this sort tend to unite and must be for a time kept apart. The new head develops on the anterior cut surface of the triangular piece, and the other head on the anterior edge of the oblique cut surface. A new pharynx develops along the posterior edge of the oblique cut in some cases, Fig. 18 and 20, in others not, Fig. 19, depending, in part, on the extent to which the pieces are kept apart after the operation, in part on the nearness of the cut to the region of the old pharynx. As soon as the two new heads have been fully formed it is seen that their size bears no relation to the fact that one has developed on the cross-cut surface and the other on the oblique surface. Their sizes depend rather on the size of the part from which they have developed, Figs. 18, and 19, and whether a new pharynx has appeared in the triangular piece, and also on the relation of the part to which they belong to the rest of the worm. The following examples may make this clearer. In the first case, Fig. 18, the triangular piece has rather a broad attachment to the other part and contains a pharynx. The larger of the two heads belongs to the old part. In the second case, Fig. 19, the triangular piece is much smaller and ends in a smaller head. It does not contain a pharynx and is attached to the other part by only a narrow area.

The third case, Fig. 20, shows that the triangular piece is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united to the other part by only a narrow connection. It contains a pharynx, and a new tail has begun to grow out near the area of attachment. This piece pulled apart later. Practically the same results were obtained when the pieces were cut as shown in Fig. 21. In this case the worm was first cut in two near the old pharynx and then by means of an oblique cut, the triangular piece was separated in such a way that a part of the old pharynx was left in each piece. A new pharynx developed in both pieces, and the same relations between the sizes of the new heads, that were described in the first and third cases above, hold here also.

Conclusions.

The results show clearly that the presence of a pharynx in a new part is an important element in the subsequent growth of the part. A part containing within itself a new pharynx behaves more like an independent worm. The most natural interpretation would be, perhaps, that this is due to the part being able to feed for itself; but while this may to some extent account for the result, yet is probably not the whole explanation. My reason for thinking so is that when the animal feeds the digestive tract of the side piece is also filled with food material. If, therefore, the planarian is kept well fed, the side piece does not lack food material even where there is no pharynx in this part.

There are some facts in connection with the mode of regeneration of planarians that may throw some light on this lack of enlargement of pieces without a pharynx. If the anterior end of a worm is cut off, the new pharynx appears, in the anterior piece, at the posterior edge of the old material. It is, at first structurally, too, the head. If the piece is fed so that the old part loses as little as possible, a new region is intercalated in front of the pharynx, and this region continues to enlarge until the normal proportions have been attained. Again, if a piece of *Planaria lugubris* is cut off behind the old pharynx, a new head arises at the anterior end, and a new pharynx, also at the anterior end just at the border between the new and the old parts. The head and pharynx are in this case also too near together, but a new region of growth is established between the head and the pharynx so

that the two are carried further and further apart. These results show that the principal growing region in the new worms lies in front of the pharynx, and it is conceivable that in the absence of the pharynx this region of growth is not formed.

The influence of the width of the region of attachment—a factor to which I ascribed some influence in my last paper—should also be taken into account here. If a pharynx is present in the part the area of union seems to play a less important rôle than when there is no pharynx present. It is probable that it is not simply the area of union as such that plays the important part, but it is the connection between the internal organs—possibly the digestive tract—that is chiefly involved in the result.

THE FORMATION OF HETEROMORPHIC HEADS IN PLANARIANS.

The formation of a heteromorphic head in *Planaria lugubris*, when the old head is cut off just behind the eyes, has been described in several of my preceding papers. In the past summer I succeeded in obtaining one such case in *Planaria maculata*, but only after a large number of trials, and furthermore in this successful case the cut was not immediately behind the eyes, as seen in Fig. 22. At the same time I cut a large number of worms into short cross-pieces, keeping all pieces of the same length together. To my surprise I found that the only pieces that produced a head at the posterior end, as well as at the anterior end (Figs. 23 and 24) were those taken just behind the old pharynx in the region of the reproductive pore. Two possibilities suggest themselves, viz., the presence of the reproductive organs in the piece, or the cut being made through the region at which this planarian pinches off pieces of itself to form new worms. If the posterior edge of the cross-piece lay in the region of constriction, where the new head of the new worm would develop, it is conceivable that this might cause the development of the heteromorphic head in the cross-piece. A similar series of cross-cuts were made on *Planaria lugubris*, but double-headed pieces were never formed on the cross-pieces from the region of the reproductive pore. In this species, however, new worms are not formed normally by pieces constricting off from the posterior end.

Neither of these possibilities seems to me to give a satisfactory

explanation of the presence of a heteromorphic head. In order to see if any internal condition is present in these double forms that may account for the results, the two preceding pieces from the posterior end, as well as two other similar pieces, were cut into sections. In three of these no pharynx was present, but parts of the old reproductive organs were present in the middle of the piece; in the fourth a pharynx was present, but the pharyngeal chamber did not open to the exterior. There was nothing in the presence of the digestive tract to give a clue as to the cause of the development of a heteromorphic head. It is true that the branches of the digestive tract were united behind, but this in itself furnishes no proof that such a union can account for the result. The sections show that a brain, nerve-cords, and eyes are present in both heads. Whatever the factors are that determine the result, the fact that the heteromorphic head appears only in short pieces will probably also have to be taken into account, for it is very improbable that a heteromorphic head would appear if whole worms were cut through in this region.

BRYN MAWR, PA., May 25, 1902.

PRELIMINARY NOTE ON THE PRESENCE OF A NEW GROUP OF NEURONES IN THE DORSAL ROOTS OF THE SPINAL NERVES OF THE WHITE RAT.

SHINKISHI HATAI.

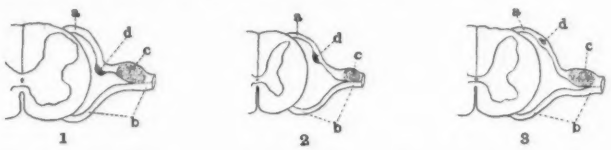
(From the Neurological Laboratory of the University of Chicago.)

While the writer was examining a large number of preparations of the spinal cord of the white rat at different ages, in order to determine whether the so-called "Hoffmann's nucleus," described recently by von Kölliker ("Weitere Beobachtungen ueber die Hoffmannschen Kerne am Mark der Vögel;" Anat. Anz., Bd. XXI., No. 3 u. 4, 1902), appears in the central nervous system of mammals, his attention was drawn to a group of nerve cells in the dorsal roots of the spinal nerves.

The spinal cord of the white rat examined does not have an isolated group of efferent neurones in the region where it was found in the spinal cord of birds. Hence the nucleus of Hoffmann is not present in this animal. A new group of cells was, however, noticed in the dorsal roots, separated from the spinal ganglia and lying between the spinal ganglion and the cord. The shape and structure of the cell-bodies found in this new group coincides with that of the cells in the spinal ganglia, and further, the size of the cells found in this group is approximately similar to that of the cells in the corresponding ganglion. The cell-body is well formed and contains one large nucleus in which one nucleolus generally, or sometimes more than one, is visible. The stainable masses are present in the cytoplasm, showing a characteristic arrangement; the latter substance stains red with eosin with the same intensity as that of the spinal ganglion cells. In every respect the cells which belong to the new group are similar in appearance to the cells of the spinal ganglion. It is easy to see that the cell bodies are surrounded by a connective tissue capsule. In some instances, the capsule is more highly developed than that of the spinal ganglion cells.

The group just mentioned has been thus far found only in the dorsal roots of young white rats having a body-weight of 4, 5, 6 and 7.5 grams respectively, and in an adult gray rat; suitable preparations from the spinal cord of the adult white rat not being at the moment available.

The exact location of the new group of cells differs at different levels of the spinal cord. The above statements on the general character of the cells found, as well as the following description, is based on a study of the young white rats alone.



Semidiagrammatic illustration of the cross section of the spinal cord of the white rat: 1, lumbar cord; 2, thoracic cord; 3, cervical cord. *a* = posterior root; *b* = anterior root; *c* = spinal ganglion; *d* = new group of the cells.

In the lumbar region, these cells lie in the dorsal root fibers rather near the spinal ganglion, where the root enlarges slightly and forms an extension ventrally (Fig. 1). This local enlargement, however, is due to the fact that at this point the dorsal root fibers take a somewhat wedge-shaped course and the nerve cells lie around the pointed tip of the wedge. The total number of the cells seems to vary according to the individual. A single section, 6 micra thick, contains usually one or two cells, though sometimes more can be seen. Since the preparations employed were not made for the purpose of the present investigation and did not form a complete series, the writer was unable to determine the total number of the cells contained in one nerve root. In one case 26 cells were counted in twenty-three successive sections through a single root.

In the thoracic region the cells are located in an enlarged portion of the dorsal root as in the lumbar region (Fig. 2). The total number of the cells in the thoracic root seems greater than in the lumbar root.

In the cervical region this cell group is slightly modified. The cell-bodies lie within the dorsal root where it exhibits a slight

enlargement (Fig. 3). In general the cell group is found nearer the cord. In this region, the group seems to contain a smaller number of the cell-bodies than at the lower levels.

From the above it is clear: First, that these cells are located within a definite region in the dorsal root, not scattered, but forming a group. Second, the cells are contained within well-developed capsules as in the case of the mature spinal ganglion cells. The latter fact shows that the cells found in this group are not at this time migrating, since migration could not occur after the formation of the capsule. The detailed investigation of this cell-group is now in progress, and the suggestion of a name for it is reserved until a more complete examination has been made.